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The fate of NH_4NO_3 added to *Sphagnum magellanicum* carpets at five European mire sites

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Abstract. Nitrogen additions as NH_4NO_3 corresponding to 0 (N0), 1 (N1), 3 (N3) and 10 (N10) g N m^{-2} yr^{-1} were made to *Sphagnum magellanicum* cores at two-week intervals *in situ* at four sites across Europe, i.e. Lakkasuo (Finland), Männikjärve (Estonia), Moidach More (UK) and Côte de Braveix (France). The same treatments were applied in a glasshouse experiment in Neuchâtel (Switzerland) in which the water table depth was artificially maintained at 7, 17 and 37 cm below the moss surface. In the field, N assimilation in excess of values in wet deposition occurred in the absence of growth, but varied widely between sites, being absent in Lakkasuo (moss N:P ratio 68) and greatest in Moidach More (N:P 21). In the glasshouse, growth was reduced by lowering the water table without any apparent effect on N assimilation. Total N content of the moss in field sites increased as the mean depth of water table increased indicating growth limitation leading to increased N concentrations which could reduce the capacity for N retention. Greater contents of NH_4^+ in the underlying peat at 30 cm depth, both in response to NH_4NO_3 addition and in the unamended cores confirmed poor retention of inorganic N by the moss at Lakkasuo. Nitrate contents in the profiles at Lakkasuo, Moidach More, and Côte de Braveix were extremely low, even in the N10 treatment, but in Männikjärve, where the mean depth of water table was greatest and retention absent, appreciable amounts of NO_3^- were detected in all cores. It is concluded that peatland drainage would reduce the capture of inorganic N in atmospheric deposition by *Sphagnum* mosses.

Introduction

The principal peat forming plants, *Sphagnum* mosses, that grow on raised bogs are adapted to use the nutrients available to them at low concentrations in rainwater. Woodin et al. (1985) demonstrated the activity of the inducable enzyme nitrate reductase in moss leaves, whereas glutamine synthetase has been identified as the dominant enzyme involved in NH_4^+ assimilation (Gerendas et al. 1997). As N inputs in wet and dry deposition have increased across Europe there is concern that the additional N inputs will affect peatland habitats through changes in vegetation or by stimulating carbon turnover (INDITE 1994). Aerts et al. (1992) reported that growth response and assimilation of inorganic-N by *Sphagnum* mosses was strongly influenced by the P concentration of the moss. Water table depth is an important factor influencing *Sphagnum* growth (Grosvernier et al. 1997) and the transformations of N in the underlying peat (Williams & Wheatley 1988), but its effect on N retention and on the fate of atmospheric N deposition has not been ascertained.

In this paper, we compare the retention of N by *Sphagnum magellanicum* (Brid.), a common and widespread moss species, to experimental applications of NH_4NO_3 at three artificially maintained water table depths in a glasshouse experiment in Switzerland and at field sites in Finland, Estonia, UK and France. The objectives of the field and glasshouse experiments were to test the hypotheses that the fate of inorganic N additions to *S. magellanicum* growing on bogs is influenced by water table depth and peat characteristics.

Materials and methods

Site descriptions

The geographical locations of the sites varied in latitude, mean annual temperature and precipitation (Table 1). The visual characteristics of the peat profiles in terms of the identifiable plant remains and degrees of decomposition of the underlying peat profile indicated a high degree of similarity between the sites (Table 2). Some characteristics of the bog and vegetation at each site are as follows:

Lakkasuo mire

The mire is located in central Finland approximately 60 km northeast of the city of Tampere, at 150 m above sea level. The average peat depth is 1.8 m and the vegetation consists of the dwarf shrubs *Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L. and *Andromeda polifolia* L. together with *Sphagnum* mosses. *S. fuscum* (Schimp.) Klinggr., *S. angustifolium* (Russ.) C. Jens and *Polytrichum strictum* (Brid) grow on hummocks and *S. magellanicum, S. balticum* (Russ.) C. Jens and *S. rubellum* (Wils.) grow in hollows with the dwarf shrubs *A. polifolia* and *Vaccinium oxycoccus* L. and *Eriophorum*

Table 1. Geographic locations, climatic characteristics and mean N inputs in rainwater of the field sites.

Site	Location	Mean Annual Temperature (Growing season) T°C	Precipitation mm yr^{-1} (season)	Mean water table depth cm (range)	N input in wet precipitation g N m^{-2} yr^{-1}
Lakkasuo	61.5°N, 24.2°E	2.9 (12)	654 (362)	5 (0–11)	0.70
Männikjärve	58.5°N, 26.2°E	4.3 (12.6)	645	38 (24–48)	0.80
Moidach More	57.3°N, 3.6°W	8.0 (11.0)	730 (368)	4 (0–11)	1.10
Côte de Braveix	45.3°N, 3.6°E	6.0 (13.6)	1150 (450)	29 (22–55)	1.05
Le Cachot	47.5°N, 6.4°E	4.7 (12)	1680 (654)	15	1.30
Neuchâtel glasshouse	46.6°N, 6.6°E	(22)		7, 17, 37	

Table 2. Visual characteristics, composition of the identifiable plant remains and degree of decomposition H (von Post 1929) in the unamended peat cores at each site.

Depth (cm)	Lakkasuo	Männikjärve	Moidach More	Côte de Braveix	Neuchâtel
0–5	*S. magellanicum*	*S. magellanicum* stems and capitulla Undecomposed stems	Live capitula & stems of *S. magellanicum, E. tetralix, T. cespitosum*	*S. magellanicum* yellow stems and leaves	*S. magellanicum*
5–10	*Sphagnum* litter remains of dwarf shrubs H1-H2	slightly decomposed stems compacted	Compressed capitula & stems of *S. magellanicum*, roots of *E. tetralix* and *T. cespitosum* H1	Weakly decomposed *S. magellanicum* H1	slightly decomposed, porous *Sphagnum* litter
10–15	*Sphagnum* peat, *Eriophorum* Dwarf shrubs	H0-H1 brown slightly decomposed stems H1	Slightly decomposed reddish stems and capitula, roots H2	light coloured *Sphagnum* peat H1	Predominantly *Sphagnum* litter, *Vaccinium oxycoccos* and *Carex* roots
15–20	H1-H3	H2	Slightly decomposed dark brown moss stems and capitula, roots H3	„ „ H2	
20–25	„ „ „	„ „ „	Slightly decomposed peat containing fibres of E. *vaginatum*	„ „	Fibrous *Sphagnum* peat H3
25–30	„ „ „	pure *Sphagnum* peat	Slightly decomposed peat, fibres of *E. vaginatum* H3/4	Yellow – brown peat H3/H4	„ „ „
30–35	*Eriophorum-Sphagnum* peat	Brown *S. magellanicum* peat with *C. vulgaris* stems and some	Partially decomposed fibrous peat H5	„ „ H5	Brown peat, H3-H4 recognisable
35–40	H3-H4	*Eriophorum* H1-H4	Amorphous peat moderately decomposed fibres H6	brown peat H6	*Sphagnum* leaves and stems
40–45	„ „ „	„ „ „	Strongly decomposed black fibrous peat H7	H7	„ „ „

vaginatum L. There is a sparse Scots pine (*Pinus sylvestris* L.) stand on the hummocks.

Männikjärve

The mire, extending to 320 ha, is located in Estonia at 79 m above sea level with a peat thickness > 4 m. The bog is a typical East-Estonian convex bog with hollows and pool complexes in the central part surrounded by pine forest. Sparse *P. sylvestris* grows on the central area, *C. vulgaris*, *Chamaedaphne calyculata* (L.) Moench. and *A. polifolia* with *E. vaginatum* dominate the dwarf shrub layer. The moss layer is predominantly formed by *S. fuscum* on hummocks, *S. magellanicum* and *S. rubellum* on hummocks and in hollows, and with *S. cuspidatum* Ehrh. ex Hoffm. and *S. majus* (Russow.) C. Jens in hollows.

Moidach More

The Moidach More is a raised bog, (National Grid Reference NJ 030420) in the north-east of Scotland, at an altitude of 275 m above sea level. The average thickness of the peat is 2.1 m and peat more than 0.5 m thick extends to 760 ha. The vegetation comprises predominantly *Sphagnum* species including *S. magellanicum*, *S. capillifolium* (Ehrh.) Hedw. and *S. recurvum* (P. Beauv.), *Erica tetralix* L. and *Trichophorum cespitosum* (L.) Hartm.. *C. vulgaris* occupies areas where there has been disturbance from peat cutting or burning.

Côte de Braveix

The Côte de Braveix mire extends to 8 ha and is located in the eastern Massif Central, France, approximately 100 km southeast of Clermont-Ferrand, at an altitude of 1350 m above sea level. The mire is typical of raised mires in the Monts du Forez region. The maximum peat thickness is about 3 m. The vegetation is dominated by *E. vaginatum* and *C. vulgaris. Carex rostrata* (Stokes) and *S. fallax* (Klinggr.) are present in places. The *Sphagnetum magellanici typicum* community is considered to be intermediate between oligotrophic fen and ombrogenous bog characterised by *S. capillifolium* hummocks with *E. vaginatum*, *T. cespitosum* and *C. vulgaris. S. magellanicum* occurs in large hummocks (0.5 to 1.0 m diameter) together with *Salix repens* L., *V. oxycoccus* and *A. polifolia.*

Neuchâtel

For the glasshouse experiment, the peat cores were taken from Le Cachot mire, situated in the Swiss Jura mountains (National Grid Reference 541.175/206.380). The mire lies at 1040 m above sea level. The peat thickness beneath intact surfaces on this small bog is up to 3–4 m depth. Vegetation consists mainly of dwarf shrubs *C. vulgaris*, *V. oxycoccus*, *Vaccinium uliginosum* L. and *A. polifolia*, together with mosses. *S. capillifolium* and *S. magellanicum* are typical of this *Sphagnetum magellanici typicum* community. Other common species are *S. fuscum* on large hummocks, *E. vaginatum*, *Polytrichum strictum* and *Aulacomnium palustre* (Hedw.) Schwaegr. The bog also supports many small *Pinus uncinata* var. *rotondata* (Link) Antoine trees.

Field experiment

The experiments were carried out in the field at Lakkasuo, Männikjärve, Moidach More and Côte de Braveix, and in the glasshouse in Neuchâtel, using a common protocol. The field and glasshouse experiments were carried out during the growing season of 1993 except in Männikjärve where the experiment was carried out in 1994. During May-June, hollow pvc cylinders (15 cm diam. and 50 cm length) were inserted into the *S. magellanicum* carpet of undisturbed bog surfaces in three replicate blocks. All other plants growing through the moss carpet were removed. The treatments were randomised within each block and at fortnightly intervals during a period of 4 months, aqueous solutions of NH_4NO_3 were applied to each core to supply the equivalent of 0, 1, 3 and 10 g N m^{-2} $year^{-1}$ (N0, N1, N3 and N10, respectively). The solutions were applied in 200 cm^3 aliquots using a syringe modified to include 6 needle outlet ports to simulate the dropwise addition of rain. To avoid edge effects, solutions were applied evenly over a quadrat, 20 × 20 cm, that contained the core at its centre. Wet N deposition was measured at each field site by collecting the rainwater every two weeks for the duration of the experiment. The height of the water table was measured with the same frequency in boreholes tubes inserted into the peat at locations adjacent to each block of cores.

Cores were excavated from the field after a period of four months. The peat core was removed from the pvc tube in the laboratory and sliced into 5 cm thick cross sections for analysis. The top 5 cm comprised mainly living *Sphagnum* moss. Each section was weighed and stored at 4 °C prior to subsampling.

Water table experiment

In the glasshouse, water table depth was artificially maintained at three levels below the surface using a purpose built apparatus (Grosvernier et al. 1997). Living, 5 cm thick, carpets of *Sphagnum magellanicum* moss collected in the field and kept at natural density were placed on the top of undisturbed peat cores (45 cm length and 15 cm diameter) contained inside PVC pots and which had been removed from beneath the *Sphagnum* carpet. The water table level was maintained at 7, 17 and 37 cm depth below the surface by connecting the pots to a Mariotte bottle (Clymo 1973).

Each treatment was replicated in three blocks giving thirty-six pots installed on three trolleys. On each trolley, the four N treatments were randomized within each of the three rows which corresponded to the three water table levels. During the experiment, the position of the trolleys in the glasshouse was randomized weekly. To reproduce daily fluctuations of humidity as experienced in the field, ie. saturation during the night and ca 40% humidity during the day (Matthey 1971), ambient air humidity was regulated using a cold deionised water vapourizer. The mosses were also humidified daily in the morning with a manual vapourizer (about 50 cm^3 per core). Pots were watered, receiving a volume of aqueous solution approximately equivalent to that added under field conditions as rain (mean annual precipitation of the field sites reported over a 4 months period). To avoid excessive temperatures during the day, shading was maintained at about 80% incident light (measured with a luxmeter), comparable to that for a *Pino-Sphagnetum magellanici* in central Europe (Neuhäusl 1975). The peat cores were extruded from the pots after a period of four months and analysed in the same way as the field cores.

Moss growth

Growth during the experiment in both the field and glasshouse was measured using the capitulum correction method (Clymo 1970). Ten to twelve *Sphagnum* plants cut to exactly 5 cm length and identified with a polyester thread, were implanted into the carpet in each cylinder. The change in dry weight (dried at 60 °C) was expressed as the mass increment per weight of original stem section, 1 cm long (Clymo 1973).

Peat analysis

Moisture contents of the cores at sampling were determined by drying weighed subsamples at 105 °C. The acidity of samples was determined by measuring pH in suspensions of fresh peat and 0.01 M $CaCl_2$ at a sample:solution ratio of 1:10 (w/v) and measurements in KCl were converted to the equivalent value in 0.01 M $CaCl_2$ using an empirical relationship derived from measurements made in both solutions.

Ammonium and nitrate were extracted by shaking freshly sampled peat (10g fresh wt) for 2 hrs with 50 cm^3 1.0 M KCl or 0.05 M K_2SO_4. Suspensions were filtered and the residue washed and made up to 100 cm^3 with distilled water.

Table 3. Total P (mg m^{-2}) contents and N:P ratio of *S. magellanicum* (0 to 5 cm) and the pH_{CaCl2}, bulk density and moisture content of the 5 to 10 cm peat layer in untreated cores from the five field sites.

	Total P	N:P ratio	pH	Bulk density g dry mass dm^{-3}	Moisture g H_2O g^{-1} dry peat
Lakkasuo	0.04	68	3.25	21.1	29.3
Männikjärve	0.71	21	3.39	12.2	10.7
Moidach More	0.20	22	2.85	22.1	16.9
Côte de Braveix	1.41	8	3.79	22.9	16.9
Neuchâtel	0.16	22	3.56	56.0	14.7
SED sites	0.04		0.07	2.27	

Chemical analyses

For total N and P, dried ground samples (150 mg) were digested in 3 cm^3 of a 1:1 mixture of conc. H_2SO_4 containing 0.1% (w/v) Se and 30% (v/v) H_2O_2 (Wall et al. 1975). Ammonium-N and phosphate-P concentrations in the acid digest were measured colorimetrically (Crooke & Simpson 1971; Murphy & Riley 1962).

Ammonium in 0.5 M K_2SO_4 extracts was diffused into 0.01 M H_2SO_4 after treatment of the extract with magnesium oxide (Bremner 1965) and the trapped NH_4-N determined colorimetrically (Crooke & Simpson 1971). Nitrate in 0.5 M K_2SO_4 extracts and in oxidized solutions was analyzed as NO_2^- after reduction with copperized cadmium (Henriksen & Selmer-Olsen 1970).

Statistical analyses

The results of the water table and field experiment were analysed separately by analysis of variance. Where comparison of field sites included the Neuchâtel experiment, values from the 17 cm water table depth were used. Incomplete analyses because of limited sample material occurred in profiles from Neuchâtel and the Côte de Braveix and the number of replicates and determinations was then restricted. For skewed distributions, as in the case of NH_4^+ and NO_3^-, values were transformed to the natural logarithm for analysis of variance, and the untransformed means and standard errors of difference presented for comparisons. These statistical analyses were performed using the Genstat 5.3 package (NAG Ltd, Oxford, UK).

Table 4. Growth, mass increment relative to the initial weight of a 1cm stem, of *S. magellanicum* at the four field sites and in the glasshouse experiment in Neuchâtel at 3 maintained water-table depths.

	Water table depth, cm	N0	N1	N3	N10	Mean
Field experiments						
Lakkasuo	5	17.7	15.0	13.0	13.3	14.8
Männikjärve	38	10.5	6.5	9.0	8.5	8.6
Moidach More	4	17.3	33.7	22.7	18.0	22.9
Côte de Braveix	29	13.3	31.3	19.2	23.8	21.9
Means		13.4	21.8	14.0	16.1	
SED		Site = 4.6, Ntrt = 3.3, Site ∗ Ntrt = 7.3				
Glasshouse	WT					
Neuchâtel	7	25.3	37.0	44.0	33.3	34.9
	17	38.7	36.3	45.7	34.3	38.7
	37	25.7	29.3	26.3	23.7	26.3
	Mean	29.9	34.2	38.7	30.4	
SED		WT = 3.5, Ntrt = 4.1, WT ∗ Ntrt = 7.1				

SED = standard error of difference of means.

Results

Visual characteristics of the peat indicated that the cores from all sites had similar degrees of decomposition (Table 2). Bulk density values for the 5–10 cm layer were broadly similar in cores from the field sites, but the peat used in the water table experiment had greater values (Table 3). Values for pH in the 5 to 10 cm layer ranged from 2.8 to 3.8 with Côte de Braveix being the least acid. Moisture contents (Table 3) at the time of sampling partly reflected the mean depth of the water table at the field sites (Table 4).

Lowering the water-table significantly ($P < 0.001$) decreased the water content of the surface moss (averaged over the N treatments) from 14.5 at 7 cm to 11.7 and 7.3 g H_2O g^{-1} dry moss at 17 and 37 cm water table, respectively (SED = 1.15, 11 d.f.). At 5–10 cm depth, the moisture content was again significantly ($P < 0.001$) decreased in the two water table treatments (11.1 and 7.6 at 17 and 37 cm, respectively compared with 15.6 at 7 cm, SED = 1.12). At 10–15 cm depth only the 37 cm water table treatment significantly ($P < 0.001$) reduced the moisture content of the peat compared with the other two treatments.

Changes in the moss layer

Growth

Averaged over the N treatments the growth of moss was significantly (P = 0.51) less in Männikjärve compared with the other sites (Table 4). The addition of N had little effect on the mean values, averaged over the four field sites, though at Moidach More and Côte de Braveix growth increased at the N1 treatment, but the site*N interaction was not significant.

Growth was greater in the water-table experiment in the glasshouse than in the field (Table 4) and lowering the water table to 37 cm below the surface significantly ($P < 0.01$) reduced growth compared with the water table depths at 7 and 17 cm depth. At these water table depths of 7 and 17 cm, the N3 treatment showed greater growth values than N0, N1 and N10, but the effects were not significant averaged over the three water table treatments and there was no significant treatment interaction.

Total N

Total N concentration of *S. magellanicum* in the surface 5 cm of N0 cores was greatest in samples from the Côte de Braveix and Männikjärve, and least in those from Moidach More (Figure 1a). Averaged over the five sites, N addition significantly ($P < 0.001$) increased the total N concentration of the moss. However, the effect was significantly ($P < 0.01$) different between the sites. In *S. magellanicum* from Männikjärve and Moidach More, total N concentrations increased linearly with increasing level of applied N, but this was not the case in the Côte de Braveix and Lakkasuo (Figure 1a).

In the water table experiment at Neuchâtel, total N concentration also increased with N addition and averaged over all three water table treatments there was a significant ($P < 0.001$) effect of NH_4NO_3 on the total N concentration of the moss tissues at N3 and N10 rates of addition compared with N0 (Figure 1b). Water table depth had no significant effect on N concentration or on the effect of NH_4NO_3 addition.

The weight of dried moss in the surface 5 cm of the cylinders showed significant ($P < 0.01$) variation between the sites and mean values were 464, 800, 912 and 650 g m^{-2} (sed = 85.0) for Lakkasuo, Männikjärve, Moidach More and Côte de Braveix, respectively. These values were not significantly altered by the addition of N. Similarly, in the water table experiment, the overall mean weight of dry moss in the surface 5 cm was 460 g m^{-2} and was unchanged by lowering the water table or additions of NH_4NO_3.

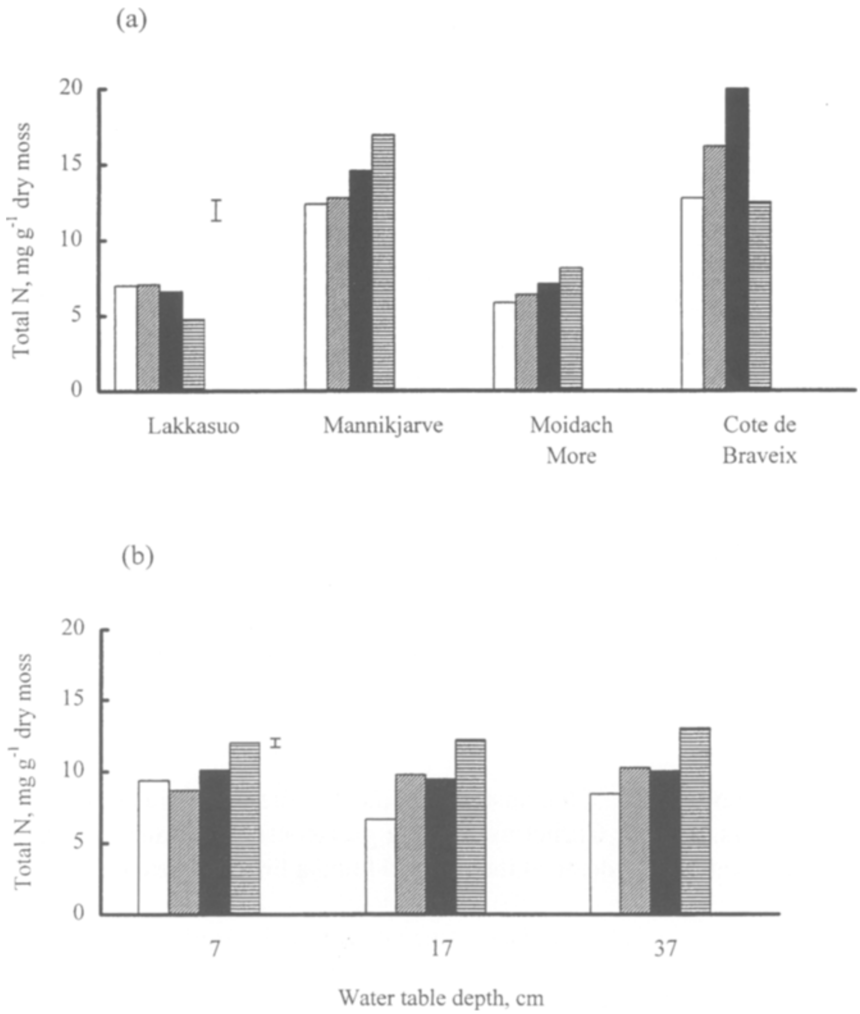

Figure 1. (a) Total N concentration (mg N g^{-1} dry moss) in the 0–5 cm moss layer from Lakkasuo, Männikjärve, Moidach More and Côte de Braveix 4 months after treatment with 0 (N0) □, 1 (N1) ▨, 3 (N3) ■ and 10 (N10) ▤ g N m^{-2} yr^{-1} every two weeks. Error bar indicates the standard error of difference (9 df) for the nitrogen × site interaction and (b) total N concentration (mg g^{-1} dry moss) in the 0–5 moss layer in the water table experiment at Neuchâtel, after 4 months with the water table depth maintained at 7, 17 and 37 cm below the surface and treatment with 0 (N0) □, 1 (N1) ▨, 3 (N3) ■ and 10 (N10) ▤ g N m^{-2} yr^{-1} every two weeks. Error bar indicates the standard error of difference between the N treatments (3 df).

Table 5. Quantities of total N (g N m^{-2}) in *S. magellanicum* in the surface 5 cm after treatment with NH_4NO_3 for 4 months at four field sites and in the glasshouse water table experiment at Neuchâtel at rates equivalent to 0 (N), 1 (N1), 3 (N3) and 10 (N10) g N m^{-2} yr^{-1}.

	N0	N1	N3	N10	Mean (sites)
Field sites					
Lakkasuo	2.7	3.1	3.6	2.6	3.0
Männikjärve	14.6	6.3	9.6	13.0	10.9
Moidach More	4.5	5.8	7.4	7.7	6.4
Côte de Braveix	10.6	13.4	9.1	7.2	10.1
Mean (Ntrt)	8.11	7.2	7.4	7.6	
SED	Sites = 1.1, Ntrt = 1.09, Site * Ntrt = 2.19				
Glasshouse					Means
Neuchâtel WT					(WT)
7 cm	4.1	4.0	4.4	5.2	4.4
17 cm	3.2	4.2	5.0	5.8	4.5
37 cm	4.1	3.8	4.6	7.0	4.9
Means	3.8	4.0	4.7	6.0	
SED	WT = 0.38, Ntrt = 0.38, WT * Ntrt = 0.65				

The total N content of the unamended moss at the four field sites plus the original moss from Le Cachot used in the glasshouse experiment correlated with mean water table depth at the site and fitted a linear regression:

$$y(\text{g N m}^{-2}) = 0.93 + 0.33 * x \text{ (mean water table depth cm)}$$

$$(R^2 = 0.79; P < 0.05)$$

The total quantities of N (g N m^{-2}) in the surface 5 cm increased progressively with the level of applied N only at Moidach More and Neuchâtel (Table 5). At the other three sites, the variability in the total N content of the moss was greater than the amounts of N added in the experimental treatments especially at Männikjärve and Côte de Braveix where the total N concentrations in the moss were also greater (Figure 1a).

In the water table experiment, the N10 addition significantly ($P < 0.001$) increased the total N content of the moss compared to the N0, N1 and N3 treatments (Table 5).

Table 6. Contents of NO_3^-, mg N m^{-2} per 5 cm layer, extracted from *S. magellanicum* in the surface 5 cm of cores at four field sites and from a water table experiment after N additions for four months corresponding to 0 (N0), 1 (N1), 3 (N3) and 10 (N10) g N m^{-2} yr^{-1} applied every two weeks as NH_4NO_3.

	N0	N1	N3	N10	Means
Field sites					
Lakkasuo	1	2	2	2	2
Männikjärve	453	239	290	587	392
Moidach More	1	2	3	2	2
Côte de Braveix	3	3	2	5	3
Means	115	62	74	149	
SED	Site = 14.5, N = 29.4, Site * N = 53.0				
Water table experiment					
Neuchâtel					
7 cm	172	232	128	116	162
17 cm	151	119	74	114	114
37 cm	92	36	94	72	74
Means	138	129	99	101	
SED	N = 36.9, WT = 31.9, WT * N = 63.8				

Retention of N by the living *Sphagnum* in the surface 5 cm was calculated as the difference between the total N content of N0 and N10 cores only because standard errors of difference between the means were large compared with the amounts added. Values were positive at only two sites, 67% and 100%, in Neuchâtel and Moidach More, respectively (Table 5). The moss at these sites had the lowest mean total N contents and greatest N retention whereas moss at Côte de Braveix and Männikjärve with the highest total N contents appeared not to retain N in the N10 treatment. In the water table experiment, mean retention of added N was 67.5%, and this capture of N was not significantly different between the water table treatments.

Extractable NH_4 and NO_3

The mean contents of NH_4^+ in the moss in the surface 5 cm of cores varied significantly ($P < 0.01$) between the sites, being greatest at Männikjärve and least at Lakkasuo (Figure 2a). Averaged over the four sites, N10 significantly ($P < 0.001$) increased the NH_4^+ contents relative to the N0, N1 and N3, and the effect was significantly ($P < 0.001$) different between the sites. In Côte

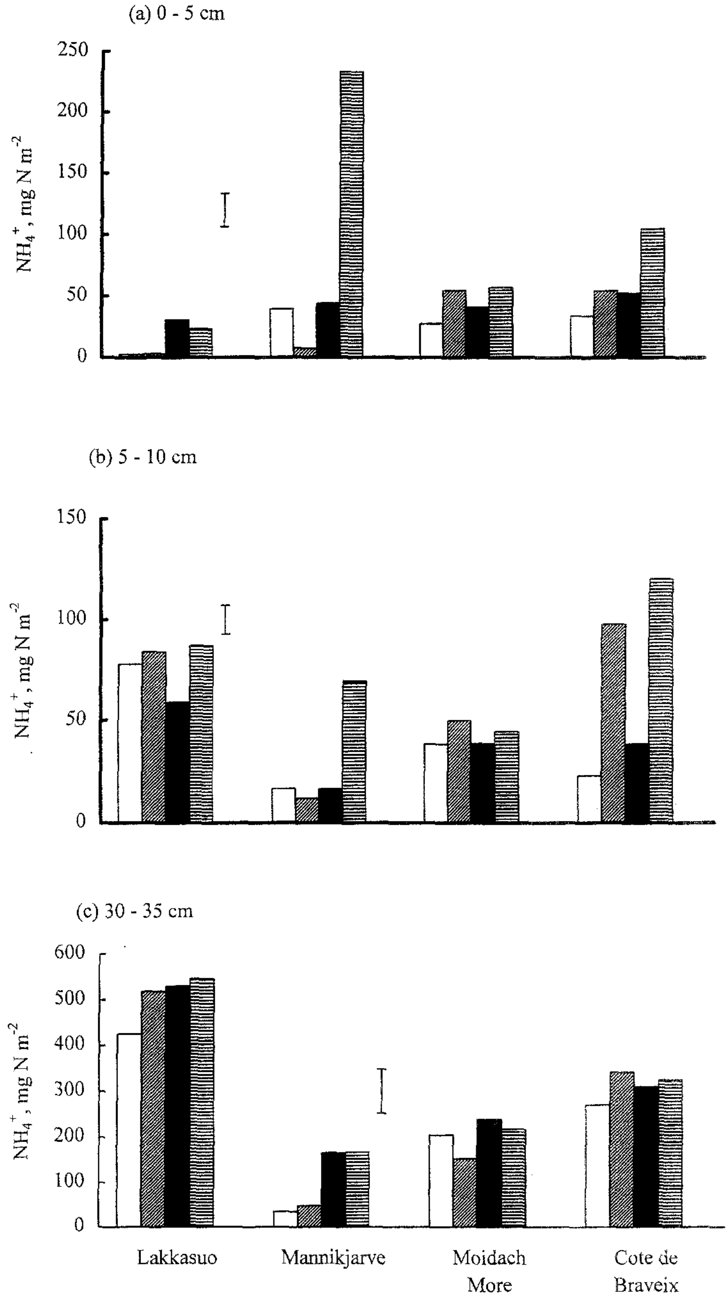

Figure 2. Ammonium contents (g N m^{-2} per 5 cm layer) in (a) the 0–5 cm, (b) the 5–10 and (c) the 30–35 cm layer of peat from Lakkasuo, Männikjärve, Moidach More and Côte de Braveix 4 months after treatment with 0 (N0) □, 1 (N1) ▨, 3 (N3) ■ and 10 (N10) ▤ g N m^{-2} yr^{-1}. Error bar indicates the standard error (9 df) of difference for the nitrogen x site interaction.

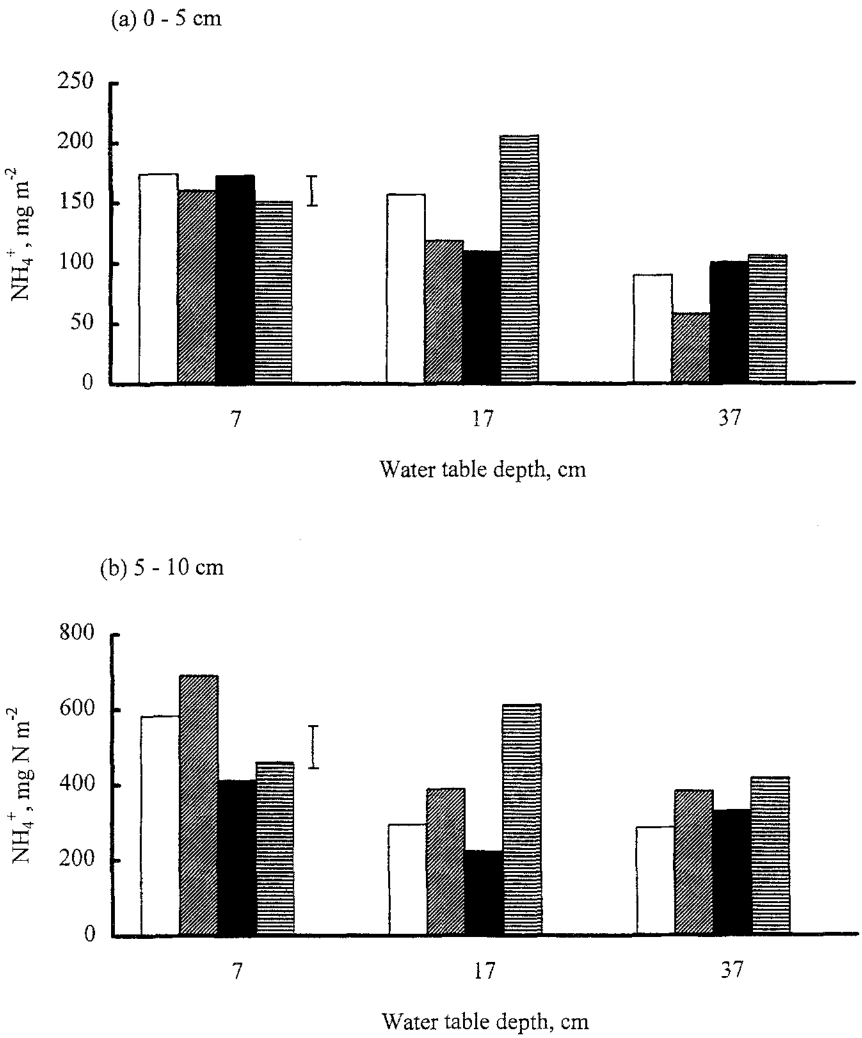

Figure 3. Ammonium contents (mg N m^{-2} per 5 cm layer) in (a) the 0–5 cm and (b) the 5–10 cm layer in the water table experiment at Neuchâtel after 4 months with the water table depth maintained at 7, 17 and 37 cm below the surface and treatment with 0 (N0) □, 1 (N1) ▨, 3 (N3) ■ and 10 (N10) ▤ g N m^{-2} yr^{-1} every two weeks. Error bar indicates the standard error of difference for the N x water table interaction (3 df).

de Braveix and Männikjärve, there was a greater accumulation of NH_4^+ in the N10 treatment than at either Lakkasuo or Moidach More.

In the watertable experiment, the mean NH_4^+ content of the unamended surface moss layer was large relative to the added NH_4^+, 140 compared with 1.7 mg N m^{-2} added and lowering the water-table to 37 cm depth significantly

($P < 0.01$) reduced the NH_4^+ content in the moss (Figure 3a). Additions of NH_4NO_3 did not alter NH_4^+ contents.

Nitrate contents of the surface moss in the four field experiments was close to the limit of detection except in Männikjärve where appreciable amounts were measured (Table 6). This difference between Männikjärve and the other sites was significant ($P < 0.001$) averaged over the N treatments. There were no significant effects of N on the NO_3^- content of the moss. Similarly, in the water table experiment, the amounts of NO_3^- in the moss were unaltered by the NH_4NO_3 addition, but values progressively and significantly ($P < 0.05$) decreased with the fall in water table from 7 to 37 cm (Table 6).

Changes in the underlying peat

Averaged across the four sites, the NH_4^+ contents at 5 to 10 cm depth were significantly ($P < 0.001$) increased by the N10 treatment, but there were no significant differences between the effects of added N at the four sites (Figure 2b). At 30–35 cm depth, the NH_4^+ content averaged over the four sites was significantly ($P < 0.01$) increased by the N10 treatment and the response was significantly ($P < 0.01$) different between the sites and was greater at Lakkasuo and Männikjärve than at Moidach More or Côte de Braveix (Figure 2c). Of the field sites, Lakkasuo contained the greatest amounts of NH_4^+ at the lower depths of both treated and untreated cores.

In the water table experiment, NH_4^+ and NO_3^-contents of the peat increased sharply, averaging 300 and 400 mg N m^{-2} in the 5–10 cm layer and lower depths and were unaffected by either the water table depth or the addition of NH_4NO_3 (Figure 3b). Compared with the field sites the contents of NH_4^+ and NO_3^- in the glasshouse experiment were much greater than the values in the field cores at the same depth (Figure 2, NH_4^+ only) which could reflect the influence of the higher temperatures in the glasshouse on net mineralization of N in the peat.

Nitrate N contents in the cores were unaffected by NH_4NO_3 additions and in samples from Moidach More, were present in trace amounts only (< 0.01 ppm in extracts). In Lakkasuo, Moidach More and Côte de Braveix, quantities of NO_3^- averaged 2 mg N m^{-2} in the 5–10 cm depth compared with 392 mg N m^{-2} at Männikjärve, and these values remained high throughout to 45 cm. depth (not shown).

The mean total quantities of NH_4^+ in the untreated cores to 45 cm depth were 2.2, 0.36, 1.3, 1.4 and 7.03 g N m^{-2} for Lakkasuo, Männikjärve, Moidach More, Côte de Braveix and Neuchâtel, respectively. For NO_3^-, the respective values were 0.37, 2.45, 0.05, 0.47 and 8.01 g N m^{-2}. The N10 treatment increased these values in Lakkasuo and Côte de Braveix such that the difference, 0.5 g N m^{-2}, between N0 and N10 for the 0–45 cm depth was 17 per cent of the added N at both sites. The same differences in Männikjärve and Neuchâtel were equivalent to 98 and 94 per cent of the added N, respectively. As no additional total N was detected in the moss at Männikjärve (Table 5) the inorganic N in the profile was probably residual NH_4NO_3 plus the existing NH_4^+ and NO_3^- present in the untreated peat. In Neuchâtel, the moss accounted for 67 per cent of the added N in the N10 treatment so that the additional N in the peat indicated net mineralization of inorganic N.

Total P

The total-P contents in the peat profiles varied markedly between the sites, being least at Lakkasuo and greatest at Côte de Braveix so that N:P ratios varied between 68 for Lakkasuo and 8 for Côte de Braveix (Table 3).

Discussion

The results of the N addition at the different field sites and in the water table experiment indicated that under some circumstances, *S. magellanicum* could assimilate more N than was present in wet deposition. As indicated by Aerts et al. (1992) the assimilation could occur without concommitant growth of the moss, leading to increased N concentrations in the plant tissues. Failure to assimilate N, as in Lakkasuo, Männikjärve and Côte de Braveix was associated either with low water table or low concentrations of P in the moss tissues. The retention of added N by *S. magellanicum* when comparing N10 with N0 was extremely variable and whereas a high N:P ratio of 68 in the moss could explain the absence of N retention at Lakkasuo (Aerts et al. 1992), this was not the case at Côte de Braveix (N:P = 8) and Männikjärve (N:P = 21) the two sites with low water table levels and high total N contents in the moss. Woodin and Lee (1987) reported that previous exposure of *S. fuscum* to atmospheric N deposition reduced its capacity to retain NO_3^-. The annual inputs of N at the five sites used in this ranged from 0.7 to 1.3 g N m^{-2} yr^{-1} and were comparable to or even higher than those at sites in Sweden with N inputs in the range 0.7 to 0.9 g N m^{-2} yr^{-1} (Aerts et al. 1992). The variable retention of total N in the N10 treatment could, therefore, be attributed to the initial total N content of the unamended moss though significant correlations between N retention and N content or concentration could not be found. If this were the case, then growth limiting factors such as low water table, could raise N concentrations in the moss and reduce the capacity to capture additional N inputs.

Results obtained in the field and the water table experiment in the glasshouse showed contrasting behaviour of *S. magellanicum* in the two environments. The average growth rates of the moss were greater in the glasshouse compared with the four field sites. While lowering the water table increased growth and reduced the amounts of extractable NH_4^+ and NO_3^- in the surface moss, in the field, the two sites with the lowest water table depth, Männikjärve and Côte de Braveix appeared to have the greatest concentrations of NH_4^+. The greater contents of the NH_4^+ and NO_3^- in the underlying peat and the greater growth rates in the glasshouse suggest an effect of the higher temperatures in the glasshouse on growth and N mineralization compared to the field during the period of the experiment. In contrast to the field sites, the cores in the glasshouse did not receive any nutrient additions in ambient rain, but the growth differences were more compatible with the effects of increased temperatues than to differences in nutrient additions from rainwater.

The behaviour of the moss at Lakkasuo and a reduced capacity to assimilate N with increasing N content implies an upper limit on the capacity of *Sphagnum* to retain N. An influence of water table depth on growth and the total N content of the moss further indicates that even where P supply is adequate N saturation in the moss could be reached sooner in sites with low water table. Peatland drainage could, therefore, have important consequences if it stimulates N concentration increases in the moss such that capture of atmospheric N is switched from the moss to the microbial processes in the underlying peat.

Hemond (1983) in a budget of N on Thoreau's Bog identified exchangeable NH_4^+ attached to cation exchange sites of *Sphagnum* as a discrete pool which is ultimately assimilated by the moss. The greater concentrations of NH_4^+ at the end of the experiment was associated with sites such as Männikjärve and Côte de Braveix where growth was not active, but the converse was not true and low concentrations and poor growth responses were evident at Lakkasuo.

Williams and Silcock (1997) reported increased amounts of extractable dissolved organic N (DON) in the *S. magellanicum* in the N10 treatment at Moidach More. This analysis for DON was not carried out at all sites, but it is quite consistent with reports of amino acid accumulation in *Sphagnum* mosses treated with NH_4NO_3 (Baxter et al. 1992). It is possible, therefore, that NH_4^+ and NO_3^- assimilated by the moss can be transformed and released to the surrounding waters as DON (Silcock & Williams 1995). The production and release of DON in the moss may be subject to influences of P and K concentrations as an addition of K_2HPO_4 to cores treated with ^{15}N labelled NH_4NO_3 stimulated ^{15}N retention and briefly reduced the concentration of DON in the moss water (Williams et al. 1998).

Greatest uncertainty surrounds the fate of inorganic N not captured by the moss layer. Where NH_4^+ was not retained, as in Lakkasuo, it reached lower depths in the profile where it could suppress microbial processes such as methane oxidation (Crill et al. 1994). The high contents of NO_3^- at lower depths in the peat in the glasshouse and at Männikjärve indicated that if denitrification was active under these conditions rates of ammonification and nitrification were so great that they exceeded the rate of NO_3^- removal. Nitrification is not commonly active in ombrogenous bogs and NO_3^- is rarely found (Hemond 1983). Denitrification as measured by N_2O production is slow under acid conditions compared to more mineral rich sites (Regina et al. 1996). Consequently, as these peats were all acid, denitrification may have accounted for some NO_3^- not retained by the moss in the wetter sites such as Lakkasuo and in the less acid peat at Côte de Braveix. At Männikjärve, where the water table depth was the greatest of the field sites, the unamended peat contained NO_3^- probably derived from atmospheric deposition which also had the highest NO_3- to NH_4-N ratio of the four field sites.

In conclusion, total N retention was close to zero in *S. magellanicum* having a wide N:P ratio and the moss behaved as though it were N saturated. Retention of N was not necessarily greater in mosses with N:P ratios < 20 and this was attributed to already higher concentrations of N in the plant tissues and a limit on the amount of N that could be assimilated by the plant. The total N content of moss at field sites increased linearly with increasing depth of the water table, a probable consequence of reduced plant growth. Hence, N saturation levels in mosses could be lowered if peatlands were drained. In the absence of N retention, NH_4^+ and NO_3^- moved to lower depths in the peat profile, though in wetter sites, the latter was absent, because of either denitrification or removal by the moss and transformation to DON which could be released into the surrounding waters.

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